PLANT AND ARTHROPOD SPECIES COMPOSITION OF SOWN AND SEMI-NATURAL PASTURE COMMUNITIES OF THREE AZOREAN ISLANDS (SANTA MARIA, TERCEIRA AND PICO)

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Recent sowed and old semi-natural pastures from three Azorean islands (Santa Maria, Terceira and Pico) were investigated in terms of plant and arthropod species composition. Semi-natural sites were shown to be well suited to reveal distinct within island trends in semi-natural pasture communities. Variation in the composition of the vascular plants follows an altitudinal gradient, which is, a dry-wet gradient, and also human influences. It is in Santa Maria, as well as in the recent sown pastures of Terceira, that the influence of human activities on vascular plant communities is most dramatic. However, for arthropods these factors seem to be less important. Variation in the species composition of arthropod assemblages within each island is less evident, and the composition of sites reflects more regional (biogeographic) factors. The results also emphasize the importance of non intensive pasture management practices in the Azores for the colonization of this habitat by endemic arthropod species. Both the vascular plant and arthropod data, subject to analysis using Sörensen's Index of Similarity reveal that, with minor exceptions, there is a clear separation of habitats only within islands. Moreover, similar overall patterns are obtained using TWINSPAN, reinforcing the importance of regional processes in shaping the arthropod composition of the Azorean pastures.

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A composição de espécies de plantas e artrópodes é estudada em pastagens recentemente semeadas e em pastagens semi-naturais de três ilhas dos Açores (Santa Maria, Terceira e Pico). As pastagens semi-naturais revelaram ser boas indicadoras de tendências próprias de cada ilha em termos de composição de espécies. A variação existente na composição de espécies de plantas vasculares segue um gradiente altitudinal, ou seja, um gradiente de secura-humidade e também algumas influências da actividade humana. É em Santa Maria que, assim como nas pastagens semeadas da Terceira que a influência humana se faz sentir com maior incidência em termos de composição de espécies de plantas vasculares. No entanto, para os artrópodes os factores humanos parecem ser menos relevantes. Não existe uma variação aparente na composição de espécies de artrópodes dentro de cada ilha, sendo a composição de espécies semelhante nos dois tipos de pastagem. A composição de espécies de artrópodes reflecte mais aspectos biogeográficos próprios de cada ilha. Notável é a presença de espécies endémicas de artrópodes nos dois tipos de pastagem, reflectindo o maneio pouco intensivo das pastagens praticado nos Açores. Através da utilização do Índice de Sörensen para a composição de espécies de plantas e de artrópodes confirmou-se que a separação entre os dois tipos de pastagem apenas se verifica dentro de cada ilha. O mesmo tipo de padrão foi obtido usando uma análise TWINSPAN, reforçando assim a

importância dos processos regionais na estructuração da composição de espécies de artrópodes nas pastagens açoreanas.

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INTRODUCTION

More than half of Azorean land is pasture of some kind (GARCIA & FURTADO 1991). Native forests have been destroyed by humans ever since the colonization of the islands for agricultural activities. After several economical cycles, and some disastrous experiences with different types of monocultures (e.g. wheat *Triticum* spp.; "Pastel" *Isatis tinctoria* L.; orange-tree *Citrus* spp.), during the second half of the 20th century cattle milk production has grown in importance. Thus, pasture is currently the dominant vegetation in this volcanic archipelago: in 1985 the estimated area of arable land in the Azores was 65.3 % of the total area; of this, 67.7% is good pastureland used for milk production, although, there is also poor arable land, mainly the high altitude, semi-natural pasture (SNP) comprising 11.2% of the total area (GARCIA & FURTADO 1991). The latter is a poorly studied community (DIAS 1997). Most SNP is located at high altitude in recent infertile acid volcanic soils (e.g. Terceira and Pico), or in more mature but still poor soils (e.g. Santa Maria).

Cattle production tends to create a uniform pastureland landscape, with plant communities dominated by introduced grasses and leguminous forbs, while native forbs (e.g. *Lotus uliginosus*), grasses, rushes, sedges and ferns are also common in the poorly managed old SNP.

DIAS (1997) described in detail all the plant communities occurring in the Azores, although little attention was paid to pasture. Surveys of the vascular plant species composition of Azorean pastures are almost confined to the works of DIAS (1986) and OLIVEIRA (1989). OLIVEIRA (1989) has shown that there are several pasture plant communities on the largest Azorean island (São Miguel) and describes five types of permanent sown pastures and two types of SNP. The most important environmental variables influencing plant species composition in the pastures from São Miguel are grazing management and altitude (including several climatic factors that are correlated with altitude) (OLIVEIRA 1989).

Both sown pastures (SP) and SNP are under cattle grazing management, but usually in the SNP the grazing pressure is concentrated in the late spring and summer. In the more intensively managed SP, grazing occurs throughout the entire year. These grazing management practices probably have an effect on the structure of both the vegetation and the arthropod fauna.

Relatively little is known of the ecology of the pastureland plants (but see DIAS 1986; OLIVEIRA 1989) and, virtually nothing about pastureland arthropod species composition and community structure in the Azores. The sample areas within the islands Santa Maria, Terceira and Pico were cattle-grazed upland pastures of two different types, recent sown pastures (3-4 years old) (SP) and wet semi-natural old pastures (more than 35 years old) (SNP). The major aim of having the two types of pasture was to detect ecological differences between improved highly productive pastures (originally sown with *Trifolium repens* L., *Lolium perenne* L. and other perennial grasses) and old semi-natural pastures. Thus, the aims of this work are: 1) to evaluate how representative of the SNP habitat within each island, are the two selected replicates of SNP from each island; 2) to characterize the selected twelve main sites (six of SP and six of SNP) in terms of plant and arthropod species composition and abundance; 3) to search for patterns in the occurrence of species in SP and SNP, or in each of the three studied islands.

MATERIAL AND METHODS

SITES AND EXPERIMENTAL DESIGN

Two replicates ("cerrados") of SP and SNP were selected in three Azorean islands (Santa Maria, Terceira and Pico) at a high-altitude level. Having taken into account that the islands have different maximum altitude, Santa Maria being the lowest altitude island and Pico the highest Azorean island, the range of altitudes of the 12 field sites lays between 290 and 800 m (see Appendix I and BORGES 1997 for a detailed description).

In all the 12 pastures (3 islands x 2 pasture types x 2 replicates), an area of at least 900 m^2 was fenced during January and February 1994 with posts and barbed wire. Rabbit fences to avoid differential rabbit grazing pressure were erected in April 1994. After the field sites were fenced, in each of them 20 3x3 (9 m^2) plots were marked with coloured small wood posts.

All field sites were grazed regularly by dairy and beef cattle, thereby maintaining the traditional management of the sites (see Appendix 1). However, I should note that due to the sampling protocol, the number of grazing periods per year in the sown pastures was lower than with usual management. Moreover, as the number of animals in the field sites of Santa Maria was lower than in the other islands, although the grazing periods were on average longer. All the sampling periods occurred at least three weeks after a grazing period, allowing regrowth of the vegetation.

Other field sites of SNP were also selected for determining the regional plant species composition in this type of habitat. In each island, together with the two main semi-natural pasture sites five other semi-natural sites were studied, two of which being the outside unfenced part of the two main semi-natural field sites (see Appendix II for a short description). It should be remarked that the outside unfenced part of the two main semi-natural field sites are not true spatially independent replicates of semi-natural pasture, but are important for determining if the two 900 m^2 fenced sites are representative of the main large pasture site. In summary, in Santa Maria the seven semi-natural sites ranged from 360 m to 500 m, in Terceira from 530 m to 560 m and in Pico from 680 m to 810 m (Appendix II). With two exceptions (site “Pico Alto” in Santa Maria and site “6.1 outs.” in Pico) all the other sites are more or less flat. Most of the 21 sites have some complex topographic characteristics due to the presence of lava tubes (e.g. Terceira and Pico) or a less intensive grazing management. All the sites were located in areas where the natural forest was cleared for pasture implementation, being the site "Mistério da Prainha" at Pico the most recent one (nine years). Consistently, all the 21 sites were under low grazing pressure, being the sites 4.2 and "4.2 outs." (Terceira) those with the improved grazing management.

Plant sampling

Three methods were used to sample the plant species:

1) *Permanent quadrats*, for which sampling occurred in spring and autumn 1994 and late summer 1995. Following partially the methodology of GIBSON et al. (1987), a wooden 1 m^2 frame, with strings to give 25 (20 x 20 cm) cells, was placed over the permanent markers of each quadrat (painted posts). In each cell, I recorded the plant species present. Within each "Cerrado", three 1 m^2 permanent quadrats were marked at random.

2) *Point-quadrats*, for which sampling occurred four times (spring, summer and autumn 1994 and summer 1995). The same frame, comprising ten equally-spaced vertical 3.00 mm diameter point-quadrat pins, used by V. K. BROWN and colleagues at Silwood Park (cf. GIBSON *et al.* 1987), was used to survey the plant species composition, abundance and structure. In each of the 20 plots, two linear frames were placed at random. The number of touches on each living plant species was recorded in 2 cm (below 10 cm) or 5 cm (10 cm and above) height intervals, to provide a measure of sward architecture. Thus, a total of 400 pins was used to sample each field site.

3) *Direct observation*, in summer and autumn 1994 and summer 1995 in each plot every vascular plant species present, in addition to those recorded by point-quadrats, were searched. The search stopped after five minutes without finding a new record. Thus, the rare species were better sampled, which takes out that the plant species present in each of the 12 field sites are known and a complete list prepared. In the spring 1995, where no point-quadrat survey was performed, a complete survey by direct observation of the plant

species present in each of the 12 field sites was also performed.

A pooled data set (see BORGES 1997) was created for vascular plant species (forbs, grasses, sedges, rushes and ferns) occurring in the 12 pasture sites, using point-quadrat and observational data obtained during five field seasons (see above). The 117 species were organized as a presence/absence matrix. I collected information on a number of characteristics for all species, namely their life-history attributes (annual, monocarpic perennial, perennial species) (FRANCO 1971, 1984) and colonization status (HANSEN 1988).

In order to access whether the SNP sites chosen are representative in the three studied islands, another five sites per island were studied (see above). For this purpose a presence/absence matrix) (see BORGES 1997) was created with data obtained during three field seasons (see above). Note that the records for each of the 21 SNP sites resulted from pooling the data of three permanent 1x1 m plots.

The families and species nomenclature follows the recent checklist of Macaronesian vascular plants of HANSEN & SUNDING (1993).

Arthropod sampling

Arthropod distributions for the 12 field sites were obtained from four complete field samples (spring, summer and autumn 1994 and summer 1995) in which pitfall traps and a mechanical suction device were used as complementary methods to survey herbivorous and predatory arthropods.

Pitfall traps

The pitfall sampling consisted of seven consecutive days (nights) of sampling in the 12 field sites. A set of twenty pitfall traps (a plastic cup with a trap diameter of 110 mm and a depth of 70 mm) was used, and positioned according to a grid structure. Each trap was dug into the ground flush with the substrate in the corner of each plot (30 cm to the inside). All four corners were used, one on each sampling occasion. The killing-preserving agent used was ethylene glycol (anti-freeze). Each trap was half-filled with the preservative with a little detergent (Teepol) added to lower the surface tension of the solution. Each trap was also protected against the rain with a white plastic dish cover fixed to the ground by three pieces of wire. The samples were stored in tubes with 70% ethanol with some drops of glycerol prior to sorting.

Suction

A "Vortis" suction apparatus (Burkhard Scientific - Sales - Ltd., Rickmansworth, Hertfordshire, England) was used to sample the pasture arthropod assemblages in the sites. The sampling on each occasion was carried out between 11.00 and 18.00, and only when the vegetation was completely dry and the wind conditions acceptable. In each of the 20 plots of each field site, four random subsamples were taken, one in each corner of the 3x3 m square plots (covering a total of 0.8 m^2). The collection nozzle was held in position for 30 seconds on each occasion. To simplify the sorting process, the four subsamples were taken successively without changing the collection vial. The samples were stored in tubes with 70% ethanol with some drops of glycerol prior to sorting.

The presence/absence pooled matrix that was obtained (see BORGES 1997) was enhanced by direct field observations of insect herbivores and spiders taken during the spring and summer 1995, with equal additional sampling effort being applied to all plots. As a result, some species less prone to being sampled by the above mentioned methods were added to the matrix (e.g. some Orthoptera and adult Lepidoptera), and the size range of other taxa was increased by these additional records. In sum, the pooled data set was based on three different sampling methods, covering three seasons, in two different years.

For each species, information was gathered on colonization status (in cases of doubt, a species was assumed to be native). The sources of information were independent for each taxonomic group, being mainly given by taxonomists expert on the Macaronesian fauna who identified the morphospecies (see a detailed list of contributions in BORGES 1997).

SPECIES ABUNDANCE DATA SETS

For the characterization of the communities in terms of densities of plant and arthropod species, the summer samples were selected, because the vegetation is at its maximum productivity at this time. The summer of 1994 was chosen in preference to that of 1995 because the latter was an atypical year (one of the rainiest years in the Azores of the last 10 years).

Vascular plants

Plant species dominance-rarity information was characterized using Importance Values (I.V.), calculated as described in Brown et al. (1987) and Evans (1988):

$$\text{Frequency of a species} = \frac{\text{Number of subplots containing a species}}{\text{Total number of subplots sampled } (= 20)}$$

$$\text{Relative frequency} = \frac{\text{Frequency of a species}}{\text{Sum of the frequency of all species}}$$

$$\text{Density of a species} = \frac{\text{Number of individuals of a species}}{\text{Area sampled } (= 180\ \text{m}^2)}$$

$$\text{Relative density} = \frac{\text{Density of a species}}{\text{Sum of the density of all species}}$$

$$\text{Relative cover} = \frac{\text{Number of touches of a species from height profile pins}}{\text{Total number of touches of all species from height profile pins}}$$

$$\text{Importance Values (I. V.) for a species} = \text{Relative frequency} + \text{Relative density} + \text{Relative cover}$$

The maximum possible importance value for a species was 300. As in BROWN *et al.* (1987), the calculation of relative density makes the assumption that, where a height profile pin is touched a number of times by a given species, only one individual of that species is sampled by that height profile pin. Observations made in the field suggested that this assumption is realistic for forbs, rushes, sedges and ferns but less so for pastureland grasses. Grasses are underestimated by this method; accordingly, for grasses every two touches on a height profile pin were considered to be an individual. Field observations confirmed this to be more realistic.

Arthropods

Arthropod abundance was assessed with a Vortis suction apparatus and is given as the number of specimens per square meter.

DATA ANALYSIS

Plants and arthropods were classified into one of three colonization categories: native, endemic and introduced. Native species arrived by natural long-distance dispersal to the Azores and are also known in other archipelagos and / or on the continental mainland. Endemic species are those that occur only in the Azores either as a result of speciation events (neo-endemics) or extinction of the mainland populations (palaeo-endemics). Introduced species are those believed to be in the archipelago as a result of human activities, some of them being exotic, cosmopolitan species.

Two methods were used to assess relationships between sites. The first was a classification method, TWINSPAN ("two-way indicator species analysis") (HILL 1979). TWINSPAN is a powerful method for summarising (GAUCH & WHITTAKER 1981) and comparing complex communities (KIKKAWA 1986). Matrices of species' presence (1) and absence (0) were classified using the default options of TWINSPAN.

The second method used Sörensen's index of similarity, C_s, a simple but reliable measure of the extent by which two sites share species in common (SOUTHWOOD 1978; MAGURRAN 1988): $C_s = 2J/(A+B)$, where J is the number of species common to the two sites and A and B are the number of species in sites A and B respectively. Three dendrograms (one for the vascular plants and the others for the herbivorous and predatory arthropods) were constructed using the method described by SOUTHWOOD (1978), in which only the highest values of similarity are used. The similarity values obtained for the herbivorous and predatory arthropods were regressed against the similarity values obtained for the vascular plant species, and the similarity values obtained for the herbivores regressed against the similarity values of predatory arthropods, looking for community resemblance across three trophic groups.

RESULTS

SPECIES COMPOSITION

Vascular plants

In the 21 SNP with permanent quadrats, a total of 84 vascular plant species were recorded, which included 8 endemic species (forbs = 5; grasses = 1; rushes = 1; ferns = 1), 29 native (forbs = 17; grasses = 1; sedges = 6; rushes = 1; ferns = 4) and 43 introduced (forbs = 26; grasses = 15; sedges = 1; rushes = 1). No obvious change in species composition was obtained with the additional SNP sites from each island, the 12 new records (eight for Santa Maria and four for Pico) being rare in the permanent quadrats. Average species richness in Santa Maria and Terceira was slightly less in the main SNP sites (Santa Maria = 31; Terceira = 21) than in the additional SNP (Santa Maria = 31.4; Terceira = 22.6). The highest difference was in Pico, where 23.5 and 28 species were recorded respectively.

The 12 main field sites (six SP and six SNP) contained a total of 117 different species of vascular plants (71 forbs, 27 grasses, 11 sedges, 3 rushes and 5 ferns), belonging to 31 families (see BORGES 1997). A total of 98 different species of vascular plants were found in the SP and 88 in the SNP. In Santa Maria more species were found in the SP (SP = 78; SNP = 58), but slightly more species were found in the SNP in Terceira (SP = 37; SNP = 41) and Pico (SP = 42; SNP = 48). A total of 27 species were found exclusively on SP (occurring 24 in Santa Maria, 5 in Terceira and 2 in Pico) and 16 species were only found in SNP (occurring 5 in Santa Maria, 7 in Terceira and 16 in Pico). From the 113 species where it was possible to determine the colonization status, eight (7%) (5 forbs, 1 grass, 1 rush and 1 fern) are Azorean endemics (2 species occurring in Santa Maria, 4 in Terceira and 6 in Pico). The average ratio native/introduced species is 0.28 for sites from Santa Maria (0.25 in the SP; 0.3 in the SNP), 0.55 in Terceira (0.2 in the SP; 0.9 in the SNP), and 0.88 in Pico (0.65 in the SP; 1.1 in the SNP).

Most of the species are perennial, the annual species occurring mainly in Santa Maria, where a drier climate favours the occurrence of this life-history group in the pastures.

Arthropods

A total of 237 arthropod species (128 herbivores and 117 predators; some species were listed as both herbivores and predators) were sampled during this study (for a complete species list see BORGES 1997). As showed elsewhere (see BORGES & BROWN 1999) the species richness of most taxa at a local scale, at a habitat scale and at an island scale is higher on Santa Maria and lower on Pico. Species richness is always intermediate on Terceira.

The main trends in introduced species are: Santa Maria = 83 spp. (44%); Terceira = 54 spp. (43%); Pico = 38 spp. (43%). Endemic species numbers and percentages in relation to the indigenous numbers were: Santa Maria = 18 spp. (17%); Terceira = 10 spp. (14%); Pico = 5 spp. (10%). Several of the sampled arthropod species are new records for the Azores or individual islands (BORGES et al. in prep.)

CLASSIFICATION OF THE SITES (TWINSPAN)

Vascular plants

The semi-natural pasture (SNP) sites

Fig. 1 shows a classification of the 21 SNP sites from the three islands studied, together with the indicator species at each division. The indicator species of Santa Maria are mostly human introductions, and those of Terceira and Pico are mainly native and endemic. A total of seven end groups were recognized by the TWINSPAN analysis. The first dichotomy made a clear separation between the 14 sites from the two islands from the central group (Terceira and Pico) and the seven sites of the older and easternmost island (Santa Maria). This first division cuts across a gradient of humidity, with the indicator species of Santa Maria being all introduced forbs and grasses well adapted to drier conditions (e.g. Crepis capillaris, Leucanthemum vulgare and Paspalum dilatatum). The indicator species of the sites from Pico and Terceira are either native (e.g. Potentilla anglica and Hydrocotyle vulgaris) or endemic (Luzula purpureo-splendens) and adapted to wetter conditions. In terms of relative abundance, none of the indicator species of the Pico-Terceira sites was particularly frequent in the permanent plots, but some of the indicator species of the seven sites from Santa Maria were particularly abundant (e.g. Arrhenatherum elatius bulbosum, C. capillaris and P. dilatatum).

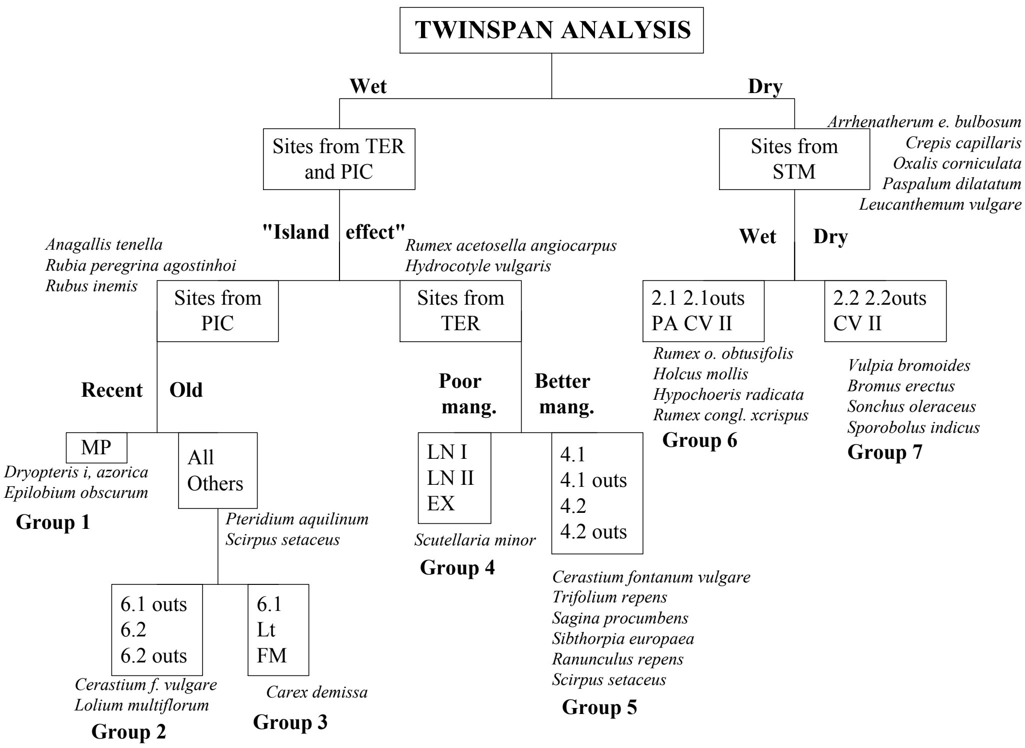

Fig. 1. Dendrogram showing the 21 permanent quadrat field sites grouped by TWINSPAN, together with the vascular plant indicator species. PIC = Pico; TER = Terceira; STM = Santa Maria; outs.= outside the fenced field site; MP = Mistério da Prainha; Lt = Longitudinal; FM = Frei Matias; LN = Lagoa do Negro; EX = Furnas do Enxofre; PA = Pico Alto; CV = Casas Velhas.

The 14 sites of the Pico-Terceira complex were divided in two groups, one with all the sites from Terceira and another with all the sites from Pico, suggesting a strong "island effect" on the structure of the vegetation.

The final seven groups may be interpreted in terms of the ecology of the indicator species and the characteristics of the sites as follows:

Group 1: includes only one site from Pico, being the most recently man-made of all 21 sites. One of the two indicator species is an Azorean endemic fern, *Dryopteris intermedia azorica*, characteristic of wet, slightly exposed habitats (SJÖGREN 1973) and the other, the native forb *Epilobium obscurum*, also prefers wet habitats in the Azores (SJÖGREN 1973). Also important, is the fact that this site is on a very recent lava flow (Mistério da Prainha), with soil mainly composed of recent basaltic rocks and highly drained.

Group 2: three sites are included, the main 6.2 site and the outside parts of the main sites 6.1 and 6.2 from Pico. Two widely distributed and common introduced pasture species are indicator species (*Cerastium fontanum vulgare* and *Lolium multiflorum*).

Group 3: the last three sites from Pico are included here, the main 6.1 site and the two other sites (Longitudinal and Frei Matias). All these three sites are lightly managed and badly drained, with the formation of "hummocks" as an adaptation of plants to periodic flooding, topographic conditions, cattle trampling or a combination of some of the former together with a fortuitous result of the morphology of some of the dominant species (e.g. the mosses *Polytrichum* spp.). *Carex demissa* is the indicator species, being one of the commonest sedges at these sites.

In the separation of Groups 4 and 5 (sites from Terceira), there is a difference in management. In fact, the three sites in Group 4 are less intensively managed than the four sites in Group 5.

Group 4: includes three sites characterized by a high cover of bryophytes as a consequence of a poor management. *Scutellaria minor* is the indicator species.

Group 5: is made up of the two main sites 4.1 and 4.2 and also by the unfenced outside parts of those sites. Six species were considered to be indicator species. *Sagina procumbens, Sibthorpia europaea* and *Scirpus setaceus* are tolerant of drought, occurring on lava flows or other dry situations, but they are also commonly found below the water level around lakes in the Azores (SJÖGREN 1973). These three species, together with *Ranunculus repens* (in wet habitats), are commonly found in other native Azorean habitats. *C. f. vulgare* and *Trifolium repens* are indicators of a more intensive management by comparison with the Group 4 sites. *S. procumbens* is included by SJÖGREN (1973) in a high altitude grassland association that also includes species like *Anthoxanthum odoratum*, *Leontodon taraxacoides longirostris*, *Lotus uliginosus*, *Plantago lanceolata*, *Potentilla anglica* and *Prunella vulgaris*, all common at these sites.

In the division of the seven sites of Santa Maria (Groups 6 and 7), there are altitude (humidity) and exposure differences. In fact, Group 6 includes the four sites located at the higher altitude (380-500 m) and protected by *Cryptomeria japonica* wind barriers, whereas Group 7 includes three semi-natural sites located at a lower altitude (360 m), but highly exposed.

Group 6: four very wet sites in Santa Maria. *Rumex obtusifolius obtusifolius* prefers wet, somewhat exposed habitats and is particularly abundant at these sites.

Group 7: three sites characterized by the presence of species adapted to drier conditions. Indicator species were the native grass *Vulpia bromoides* and the anthropochorous species *Bromus erectus*, *Sonchus oleraceus* and *Sporobolus indicus*.

In a phytosociological classification, the SNP sites from Terceira and Pico may be classified as "*Polytricho-Holcetum*" (OLIVEIRA 1989) but with also a predominance of *Agrostis castellana*. The sites from Santa Maria do not fit into the phytosociological groups defined by OLIVEIRA (1989) for São Miguel.

The 12 main sites

The separation obtained between the sites [1.1, 1.2, 2.1, 2.2 (Santa Maria), 3.1, 3.2 (Terceira)] and [4.1, 4.2 (Terceira), 5.1, 5.2, 6.1, 6.2 (Pico)] (Fig. 2) follows a gradient of humidity and altitude. Indeed, the first six sites (1.1 to 3.2) had less rainfall during the years of 1994 and 1995 than the remainder (see BORGES 1997), the values of precipitation obtained being highly correlated with the altitude of the sites (log rainfall = 0.63 + 0.93 log altitude, $n = 10$, $r = 0.75$, $p = 0.01$ for 1994; log rainfall = 0.05 + 1.22 log altitude, n =

10, r = 0.94, p = 0.0001 for 1995) (Note that only ten data points were used, since in Santa Maria only two metereological stations were available). From the indicator species of the wet sites (Fig. 2), two are endemics (*Lysimachia azorica* and *L. purpureo-splendens*) and the other four are native species all adapted to moist, acidic habitats. The indicator species from the drier sites are common anthropochorous species. Four of these species (excluding *Cyperus rotundus*) are very common at the four sites from Santa Maria, but rare at the two drier sites from Terceira (3.1 and 3.2).

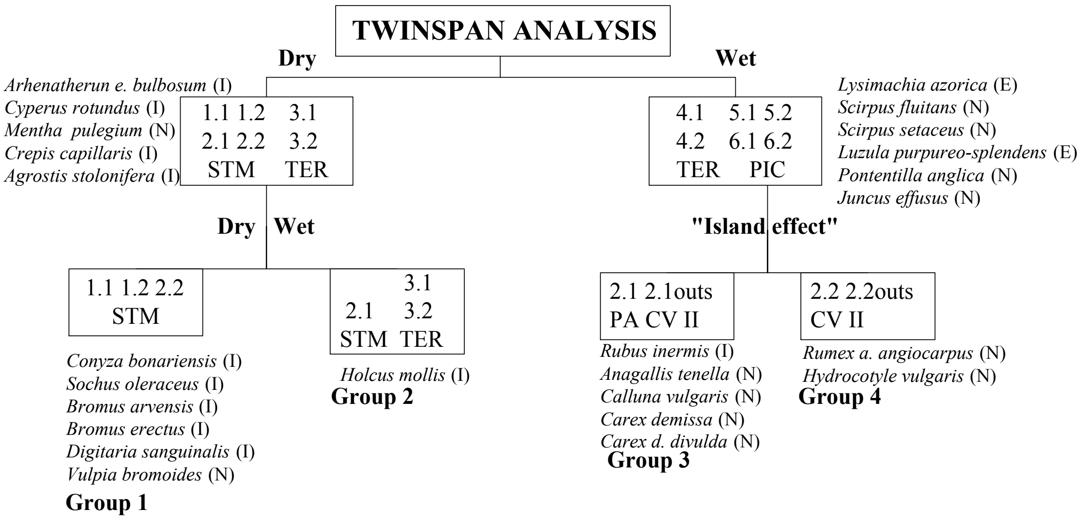

Fig. 2. Dendrogram showing the 12 main field sites grouped by TWINSPAN, together with the vascular plant indicator species. PIC = Pico; TER = Terceira; STM = Santa Maria; N = Native; E = Endemic; I = Introduced.

TWINSPAN identified four groups. The drier sites were split also according to differences in humidity and elevation, including the high altitude SNP of Santa Maria (2.1, Fontinhas) together with the two drier sites from Terceira (SP 3.1 and 3.2, Altares), in spite of belonging to different pasture habitat types; the other six sites (SNP sites from Terceira and all sites from Pico) were grouped in terms of island identity (regional scale).

Group 1: comprised two SP (1.1 and 1.2) and the driest SNP site from Santa Maria (2.2). With the exception of *V. bromoides*, all the indicator species are exotic anthropochorous species. All the indicator species are adapted to sandy soils and dry conditions, and are not particularly abundant. The most dominant species in terms of Importance Values are summarized in Table 1. SP site 1.1 is characterized by a high dominance of the weed *P. lanceolata*, but also by the sown species *L. multiflorum* and *T. repens*. The legume *T. repens* together with the grass *Elytrigia repens* dominate at SP 1.2. SNP site 2.2 is characterized by a high dominance of the weedy forb *P. lanceolata* and the grasses *L. multiflorum* and *H. lanatus*.

Table 1
Summary of the 21 dominant vascular plant species based on Summer 1994 Importance Values (I.V.) (see text). The dominant species (I.V. > 10) in each site are in bold.

	Sown		Semi-natural		Sown		Semi-natural		Sown		Semi-natural	
	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2
Agrostis castellana	0	0	**53.64**	6.21	0	0	**127.34**	**112.94**	**79.91**	**35.12**	**71.73**	**61.58**
A. stolonifera	**11.49**	0	0	0	**24.00**	**13.04**	0	0	0	0	0	0
Anthoxanthum odoratum	2.26	0.74	3.23	8.51	0	0	4.71	**25.03**	**18.44**	**19.93**	**60.43**	**58.86**
Arrhenatherum e. bulbosum	0	1.48	4.59	2.69	**19.58**	3.63	0	0	0	0	0	0
Crepis capillaris	8.30	2.07	**18.50**	**26.89**	0	0	0	0	0	0	0	0
Cyperus rotundus	0	0	0	0	**12.13**	**13.84**	0	0	0	0	0	0
Dactylis g. glomerata	0	0	0	0	0	0	0	0	**12.62**	**30.33**	0	0
Elytrigia repens	0	**87.35**	0	0	**13.16**	0	0	0	0	0	0	0
Holcus lanatus	0.79	**20.46**	**49.39**	**38.01**	**141.95**	**156.37**	**30.35**	**35.31**	**15.73**	**44.08**	**49.48**	**68.30**
Hydrocotyle vulgaris	0	0	0	0	0	0	**15.73**	0	0	0	0	0
Leontodon t. longirostris	2.81	1.79	9.82	**26.56**	0	0	7.52	8.53	8.03	5.77	**15.00**	1.74
Lolium multiflorum	**48.77**	**12.90**	7.55	**32.69**	0	1.75	0	4.32	3.16	**10.14**	0	0.62
L. perenne	**23.49**	**20.63**	0	0.43	7.26	**13.44**	0	2.34	**60.29**	**62.98**	0	0
Lotus uliginosus	0	0	**56.77**	**28.25**	**21.64**	0	**36.93**	**26.00**	**13.54**	**15.01**	**36.05**	**16.30**
Mentha suaveolens	0	0	0	0	**18.25**	**25.62**	0	0	0	0	0	0
Paspalum dilatatum	**19.50**	0	0.47	8.07	0	0	0	0	0	0	0	0
Plantago lanceolata	**57.91**	3.59	**19.09**	**41.28**	0	5.99	1.59	3.39	2.72	8.00	**10.68**	**11.85**
Poa trivialis	**10.02**	4.70	5.97	**10.80**	8.90	**10.58**	**17.74**	**17.41**	**45.98**	**27.24**	**16.32**	**16.21**
Potentilla anglica	0	0	0	0	0	0	8.23	2.32	0.59	2.60	3.86	**13.16**
Rumex a. angiocarpus	0	0	8.72	0	**12.53**	6.83	4.35	**20.74**	0	0	0	0
Trifolium repens	**63.90**	**107.22**	4.45	**20.20**	**13.35**	**42.50**	**10.10**	**14.21**	**38.67**	**10.94**	0.55	0.81

Group 2: includes the two SP sites from Terceira and the SNP site from Santa Maria located at the highest altitude (site 2.1), that is, with similar annual rainfall and mean temperature. However, these three sites differ greatly in species richness and relative abundance, but were grouped mainly as a consequence of having a different vascular plant species composition different to sites 1.1, 1.2 and 2.2.

SNP site 2.1 is characterized by a high dominance of grasses *A. castellana* and *H. lanatus*, but also by the native legume *L. uliginosus*, while the SP 3.1 and 3.2 are dominated by the grass *H. lanatus* (see Table 1). The legume *T. repens* is also an important species in site 3.2.

Group 3: all the sites from Pico were included in this group. Only one of the indicator species from Pico is particularly abundant, the introduced species *Rubus inermis*, but only at one site (6.2). All the other four species are native to the archipelago and not particularly common at the sites. Two of the indicator species, *Anagallis tenella* and *Calluna vulgaris*, are included in the phytosociological association "*Anagallidetum tenellae*" (SJÖGREN 1973) that also includes species commonly found in these sites, such as *A. castellana*, *A. odoratum*, *L. purpureo-splendens*, *Prunella vulgaris*, *Scirpus fluitans* and *Vaccinium cylindraceum*. Most of the indicator species prefer wet, very exposed habitats.

SP sites 5.1 and 5.2 are characterized by a high dominance of the grasses *A. castellana* and *L. perenne. Poa trivialis* and *T. repens* in site 5.1 and *H. lanatus* in site 5.2 are also dominant species (see Table 1). The two SNP from Pico (sites 6.1 and 6.2) are characterized by a high dominance of the grasses *A. castellana*, *A. odoratum* and *H. lanatus*, and the native legume *L. uliginosus* (Table 1).

Group 4: the two SNP sites from Terceira were grouped together. The indicator species *Hydrocotyle vulgaris* is a characteristic species from SNP wet sites at Terceira. *R. a. angiocarpus* is quite abundant at site 4.2 (see below).

SNP sites 4.1 and 4.2 are characterized by high dominance of the grasses *A. castellana* and *H. lanatus* and the native legume *L. uliginosus*. Also common are the grass *A. odoratum* and the weedy forb *R. a. angiocarpus* (site 4.2) (Table 1).

Arthropods

As in the classification of vascular plants, four end groups were also derived from the TWINSPAN analysis, using the presence-absence matrix of herbivorous arthropods from the 12 main field sites (Fig. 3a). However, only two of the groups are equivalent to those obtained for the vascular plants (Groups 3 and 4 in Fig. 2 and Groups 2 and 3 in Fig. 3a). The first dichotomy separated the islands in the Central group (Pico and Terceira) from the eastern island (Santa Maria). There is no consistent indicator species of the Pico-Terceira complex. The eight sites of the Pico-Terceira complex were split further into two groups, a group containing the moist sites (all four from Pico and the semi-natural sites from Terceira) and a group containing the drier sites from Terceira (SP 3.1 and 3.2).

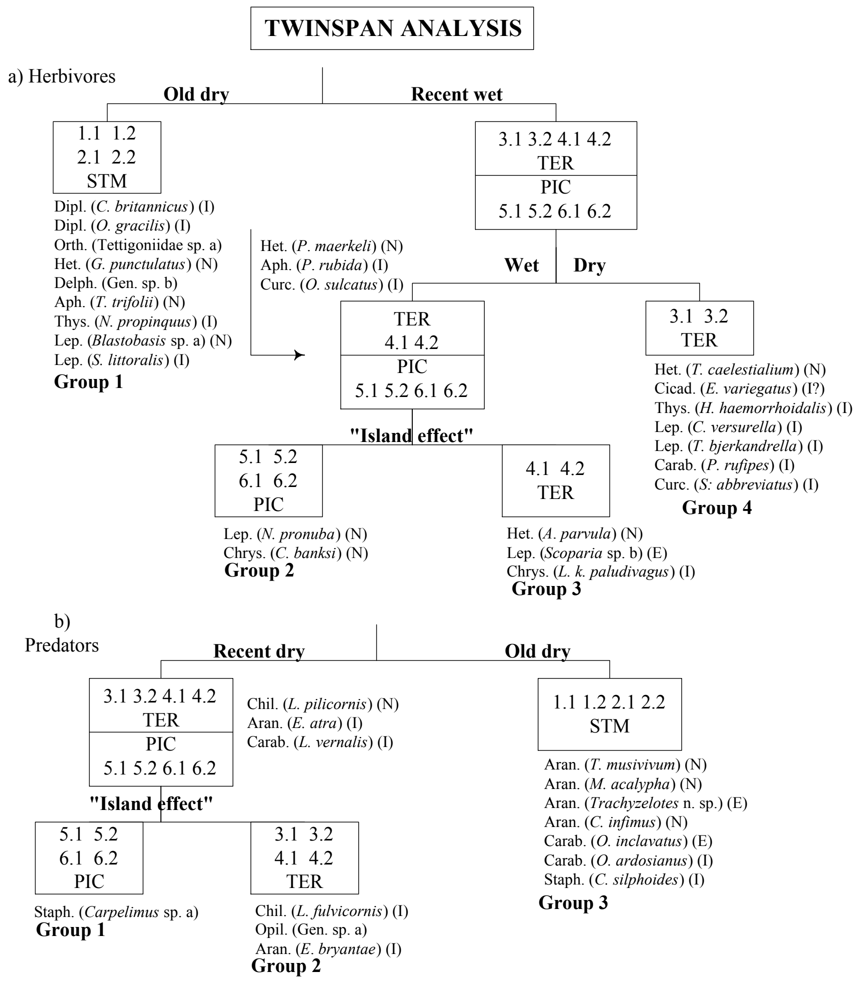

Fig. 3. Dendrogram showing the 12 main field sites grouped by TWINSPAN, together with the indicator species. a) Herbivores; b) Predators. PIC = Pico; TER = Terceira; STM = Santa Maria; N = Native; E = Endemic; I = Introduced. Dipl. = Diplopoda; Orth. = Orthoptera; Het. = Heteroptera; Cicad. = Cicadellidae; Delph. = Delphacidae; Aph. = Aphididae; Thys. = Thysanoptera; Lep. = Lepidoptera; Chrys. = Chrysomelidae; Curc. = Curculionidae; Chil. = Chilopoda; Opil. = Opiliones; Aran. = Araneae; Carab. = Carabidae; Staph. = Staphylinidae.

Group 1: all the sites from the easternmost, older island Santa Maria were grouped together. Nine species are indicator species, comprising a heterogeneous group that includes two exotic millipede species (generalist root-feeders), the native burrowing-bug *Geotomus punctulatus* (root-feeder) (Heteroptera, Cydnidae), the native aphid species *Therioaphis trifolii* (legume-feeder), the introduced thrip *Nesothrips propinquus* (generalist grass and sedge-feeder), two generalist-feeding moths (*Blastobasis* sp. a and *Spodoptera littoralis*), a delphacid species (Gen. sp. b) and the bush cricket Tettigoniidae sp. a. Only the aphid species was particularly abundant on the sites. The most abundant species of herbivores on these sites in the summer 1994 are summarized in Table 2a. *Aptinothrips rufus* (Thysanoptera) was very common in all the four sites, being *Euscelidius variegatus* (Hom. Cicadellidae) common in the drier sites 1.1, 1.2 and 2.2 (Table 2a). SNP 2.1 is characterized by high densities of *Megamelodes quadrimaculatus* (Hom. Delphacidae) (64.2 m-^{2}) and *Muellerianella* sp. a (Hom. Delphacidae) (62.7 m^{-2}), being the latter species also very common in the other SNP (2.2). *T. trifolii* (Hom. Aphididae) attained high densities (33.9 m^{-2}) but only in SP 1.2 (see Table 2a).

Table 2

Summary of the 34 most abundant arthropod species (herbivores = 10 species; predators = 14 species) based on Summer 1994 densities (number of specimens per square meter). The four or five most abundant species of herbivores (a) and predators (b) in each site are in bold.

	Santa Maria				Terceira				Pico			
	Sown		Semi-natural		Sown		Semi-natural		Sown		Semi-natural	
	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2	6.1	6.2
a) HERBIVORES												
?? *Acalypta parvula*	0	0	0	0	0	0	**3.13**	0.25	0	0	0	0
Acyrthosiphon pisum	**7.75**	**2.56**	**8.94**	**3.31**	1.19	**2.31**	0.13	0.38	**1.06**	**1.13**	0.94	0.56
Anoscopus albifrons	0.06	1.06	2.44	**4.75**	0.25	1.75	**2.88**	**9.69**	**0.50**	0.94	**1.75**	**1.50**
Aptinothrips rufus	**11.13**	**10.75**	**10.38**	**9.13**	**31.31**	**21.94**	**15.25**	**2.06**	**20.56**	**17.25**	**22.38**	**26.88**
Euscelidius variegatus	**10.38**	**6.00**	0.06	**17.19**	**14.13**	**31.88**	0	0	0	0	0	0
Macrosteles sexnotatus	0	0	2.06	0	**1.25**	0.25	0.06	0.38	0	0	0	0
Megamelodes quadrimaculatus	0	0.06	**64.19**	0.13	0.06	0.06	**4.44**	**0.50**	0.06	**2.06**	**1.25**	**2.56**
Muellerianella sp. a	2.06	1.31	**62.69**	**28.69**	**8.44**	**6.50**	**2.63**	0.31	0	0.94	0.75	**2.44**
Mythimna unipuncta	**2.44**	**1.56**	**5.56**	3.19	**6.13**	**9.75**	2.25	**4.00**	**2.00**	**1.44**	**3.00**	**5.56**
Therioaphis trifolii	**2.69**	**33.94**	0.19	1.06	0	0	0	0	0	0	0	0
b) PREDATORS												
Achaearanea acoreensis	0.19	0.25	0.31	**0.50**	0	0.13	0	0.25	**0.75**	0.13	0.56	**0.94**
Aeolothrips fasciatus	1.25	**1.94**	**0.63**	**0.63**	0.13	0	0	0	0	0	0	0
Amisha analis	0.69	**1.75**	0	0.44	**4.38**	**2.56**	**3.00**	**1.06**	**5.69**	**6.88**	**4.88**	**3.75**
Atheta (*Mocyta*) *fungi*	0	0.06	**1.81**	0	0	0	0	0	0	0	0	0
Cilea silphoides	**1.75**	0.25	0.31	**0.50**	0	0	0	0	0	0	0	0
Erigone atra	0	0	0	0	0.13	0.31	**4.75**	**2.06**	**2.31**	**3.81**	**1.00**	**2.25**
Erigone autumnalis	**1.88**	**2.00**	0	1.13	0.06	**0.88**	**1.75**	**3.06**	**2.06**	**0.56**	0	0.31
Erigone dentipalpis	**2.63**	0.88	0.31	**2.19**	**0.25**	0.38	0.25	0.13	0.56	0	**1.56**	0.56
?? *Lamyctes fulvicornis*	0	0	0	0	0.19	0.06	0.13	**1.06**	0	0	0	0
Leptyphantes tenuis	**2.50**	0.81	**8.19**	**2.19**	**0.25**	**0.56**	0.50	**1.44**	**2.25**	**3.25**	**1.81**	**2.13**
Oedothorax fuscus	0.06	0	0	0	**4.81**	**8.56**	**2.81**	**5.25**	0	0	0	0
Oligota parva	0.63	**1.06**	0	0.06	0	0	0	0	0	0	0	0
Opiliones (Gen. sp. a)	0	0	0	0	**0.63**	**2.13**	0	0	0	0	0	0
Sunius propinquus	**1.56**	0.69	0	0.06	0	0	0	0	0	0	0	0

Group 2: the four sites from Pico were grouped together, with the indicator species being two generalist native species, the common root-feeding moth *Noctua pronuba* and the leaf-feeding chrysomelid beetle, *Chrysolina banksi*. The most abundant species of herbivore in these sites in the summer 1994 was *A. rufus* (Thysanoptera) (>> 17 m-^{2}), but *Mythimna unipuncta* (Lep. Noctuidae) (all the sites), *M. quadrimaculatus* (Hom. Delphacidae) (sites 5.2

and 6.2) and *Muellerianella* sp. a (Hom. Delphacidae) (site 6.2) were also abundant (Table 2a).

Group 3: contained the two SNP sites from Terceira. Indicator species are the native lace-bug (*Acalypta parvula*), the endemic moth *Scoparia* sp. b and the introduced leaf-feeding chrysomelid beetle *Longitarsus kutscherae paludivagus*. The lace-bug and the moth are abundant on the sites. The most abundant species in the summer 1994 were not the same in the two sites. In fact, *A. rufus* (Thysanoptera), *M. quadrimaculatus* (Hom. Delphacidae) and *A. parvula* (Het. Tingidae) in site 4.1, and *Anoscopus albifrons* (Hom. Cicadellidae) and *M. unipuncta* (Lep. Noctuidae) in site 4.2 were the most abundant species (Table 2a).

Group 4: contained the two SP sites from Terceira. Most of the indicator species are human introductions to the Azores and are very abundant at these two sites. The moth *Tebenna bjerkandrella* is a specialist feeder of the weed *Mentha suaveolens* a species particularly common at these sites. With the exception of the thrip *Heliothrips haemorrhoidalis*, all the other indicator species (see Fig. 3) are grass-feeders, which reflects the dominance of grasses at the sites. *A. rufus* (Thysanoptera) and *E. variegatus* (Hom. Cicadellidae) were the most abundant species of herbivores in the summer 1994 in these sites, but *M. unipuncta* (Lep. Noctuidae) and *Muellerianella* sp. a were also common (see Table 2a).

TWINSPAN (Fig. 3b) identified only three groups based on the predatory arthropods. The groups represent the separate islands. As with the analysis of herbivorous species, the first division contrasted the islands in the central group (Pico and Terceira) with the eastern island (Santa Maria). The indicator species of the Pico-Terceira complex contains two very abundant species, the linyphiid spider *Erigone atra* and the ground-beetle *Lagarus vernalis* (Pitfall data, pers. obs.); the chilopod lithobiomorph *Lithobius pilicornis* is also the commonest of all the centipedes.

Group 1: is formed by the four sites from Pico. The indicator species is a bark rove-beetle *Carpelimus* sp. a, probably living in the indigenous shrubs *Calluna vulgaris*, *Erica scoparia azorica* and *Vaccinium cylindraceum*. The most abundant predatory arthropods were *Amisha analis* (Staphylinidae), *E. atra* (Araneae) and *Lepthyphantes tenuis* (Araneae) in all the four sites, but *Erigone autumnalis* (Araneae) (site 5.1) and *Erigone dentipalpis* (Araneae) (site 6.1) were also common (see Table 2b).

Group 2: all the sites from Terceira were grouped together. All the three indicator species are not particularly abundant and are probably human introductions. The most abundant predatory arthropods from these four sites were *Oedothorax fuscus* (Araneae) and *A. analis* (Staphylinidae), but *E. atra* (Araneae) and *E. autumnalis* (Araneae) are also abundant in the two SNP sites (see Table 2b).

Group 3: finally, the four sites of Santa Maria were also grouped together. Four species of spiders, two species of ground-beetles and one species of rove-beetle were found only on this island and were selected as indicator species. Two species are endemic to the island (the wandering spider *Trachyzelotes* n. sp. and the ground-beetle *Olisthopus inclavatus*), three species are native and two are introduced. All seven indicator species were never abundant at the sites, but were sampled on most sampling occasions. The only predatory arthropod species common in the four sites was *L. tenuis* (Araneae). Also abundant were *E. dentipalpis* (Araneae) (sites 1.1 and 2.2), *E. autumnalis* (Araneae) (SP 1.1 and 1.2), *Cilea silphoides* (Staphylinidae) (site 1.1), *Atheta fungi* (Staphylinidae) (site 2.1), and *Aeolothrips fasciatus* (Thysanoptera) and *A. analis* (Staphylinidae) (site 1.2) (see Table 2b).

Similarity between sites

Using the Sörensen's Index of Similarity the affinity between sites was calculated using data for vascular plants (Table 3), herbivorous arthropods (Table 4) and predatory arthropods (Table 5). The results are summarized in three dendrograms (Figs 4, 5a and 5b).

Table 3

Diagram showing the numbers of vascular species in common (upper triangle) and Sörensen's Index of Similarity values (lower triangle) between all possible paired sites, using the presence/absence list of species. The similarity values for the comparisons between replicates are shown in bold.

	1.1	**1.2**	**2.1**	**2.2**	**3.1**	**3.2**	**4.1**	**4.2**	**5.1**	**5.2**	**6.1**	**6.2**
1.1		43	31	43	22	27	18	20	20	20	17	20
1.2	**0.71**		23	34	18	23	14	15	17	17	15	15
2.1	0.56	0.51		32	17	21	15	15	17	16	16	16
2.2	0.72	0.67	**0.71**		20	26	15	18	20	19	16	18
3.1	0.45	0.46	0.51	0.52		23	15	17	15	14	12	15
3.2	0.52	0.55	0.58	0.63	**0.77**		15	18	20	18	15	18
4.1	0.34	0.33	0.40	0.35	0.48	0.44		26	23	26	27	27
4.2	0.39	0.36	0.42	0.44	0.58	0.55	**0.78**		20	22	20	22
5.1	0.38	0.39	0.45	0.47	0.48	0.58	0.65	0.59		30	27	29
5.2	0.38	0.39	0.42	0.44	0.44	0.52	0.73	0.65	**0.83**		25	28
6.1	0.31	0.33	0.41	0.36	0.36	0.42	0.73	0.56	0.72	0.67		30
6.2	0.37	0.33	0.41	0.40	0.45	0.50	0.73	0.62	0.77	0.75	**0.77**	

Table 4

Diagram showing the numbers of herbivorous arthropod species in common (upper triangle) and Sörensen's Index of Similarity values (lower triangle) between all possible paired sites, using the presence/absence list of species. The similarity values for the comparisons between replicates are shown in bold.

	1.1	**1.2**	**2.1**	**2.2**	**3.1**	**3.2**	**4.1**	**4.2**	**5.1**	**5.2**	**6.1**	**6.2**
1.1		43	48	53	32	33	19	25	20	17	19	18
1.2	**0.66**		43	44	26	25	15	19	18	15	16	17
2.1	0.69	0.69		52	26	30	19	25	23	19	20	19
2.2	0.74	0.68	**0.75**		30	33	20	25	23	20	22	20
3.1	0.57	0.53	0.49	0.54		33	18	23	18	16	17	15
3.2	0.56	0.49	0.54	0.57	**0.79**		17	22	22	18	20	16
4.1	0.38	0.35	0.40	0.41	0.54	0.48		24	16	18	18	17
4.2	0.45	0.40	0.48	0.46	0.60	0.54	**0.75**		20	19	20	20
5.1	0.40	0.42	0.48	0.46	0.53	0.61	0.58	0.62		20	19	19
5.2	0.34	0.35	0.40	0.40	0.47	0.50	0.65	0.58	**0.71**		21	21
6.1	0.38	0.38	0.43	0.45	0.51	0.56	0.67	0.63	0.69	0.76		19
6.2	0.37	0.41	0.41	0.42	0.46	0.46	0.65	0.65	0.72	0.79	**0.73**	

Table 5

Diagram showing the numbers of predatory arthropod species in common (upper triangle) and Sörensen's Index of Similarity values (lower triangle) between all possible paired sites, using the presence/absence list of species. The similarity values for the comparisons between replicates are shown in bold.

	1.1	**1.2**	**2.1**	**2.2**	**3.1**	**3.2**	**4.1**	**4.2**	**5.1**	**5.2**	**6.1**	**6.2**
1.1		43	29	40	34	30	19	24	19	21	18	20
1.2	**0.75**		28	38	31	28	18	23	19	20	17	19
2.1	0.57	0.56		29	23	22	15	19	17	20	16	19
2.2	0.72	0.70	**0.60**		31	32	18	24	20	23	20	22
3.1	0.65	0.61	0.51	0.63		35	25	31	23	25	23	25
3.2	0.61	0.58	0.52	0.68	**0.80**		23	29	21	24	21	23
4.1	0.40	0.39	0.37	0.40	0.60	0.59		29	23	21	20	21
4.2	0.49	0.48	0.46	0.52	0.73	0.73	**0.76**		24	25	24	27
5.1	0.42	0.43	0.45	0.47	0.59	0.58	0.67	0.68		26	24	25
5.2	0.45	0.44	0.51	0.52	0.62	0.63	0.58	0.68	**0.78**		24	27
6.1	0.40	0.39	0.42	0.47	0.59	0.58	0.58	0.68	0.75	0.72		27
6.2	0.44	0.43	0.49	0.51	0.63	0.62	0.60	0.75	0.77	0.79	**0.83**	

For the vascular plants (Fig. 4, see also Table 3), the two main groups of sites are the same as those obtained in the first dichotomy of the TWINSPAN analysis (see Fig. 2). The SNP sites from Terceira are also grouped and separated from the Pico sites. The main difference in relation to the TWINSPAN results is the maintenance of island identity for the drier sites, with the two sites from Terceira (3.1 and 3.2) being separated from the four sites of Santa Maria. However, the most important result is the consistently high similarity between almost all the replicates. The exception occurred in Santa Maria, where the SP and the SNP are still highly similar, but one of the SP (1.1) is even more similar to one of the SNP (2.2).

When the herbivores are used, the same dichotomies and groups of sites obtained previously in the TWINSPAN analysis (Fig. 3a) were obtained in the similarity dendrogram (Fig. 5a). Again, Santa Maria is isolated from Terceira and Pico, and the SP from Terceira are less related to the other six sites (all from Pico and the two SNP sites from Terceira). Predatory arthropods also generate a dendrogram (Fig. 5b) consistent with the TWINSPAN analysis (see Fig. 3b), with Terceira and Pico grouped together and Santa Maria isolated. Again, there is one exception; whilst the high similarity between replicates is noticeable, and there is a clear separation between the two pasture types in Terceira and Pico, the SNP site 2.1 from Santa Maria is obviously different, reflecting the occurrence of a large set of unique predatory species at this site.

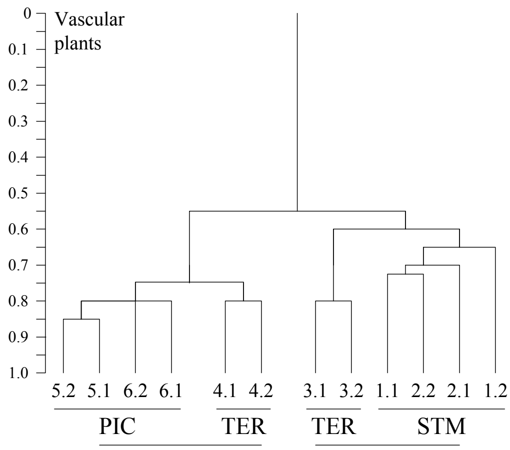

Fig. 4. A dendrogram of similarity (Sörensen's Index of Similarity) using the vascular plant species (data in Table 3). PIC = Pico; TER = Terceira; STM = Santa Maria.

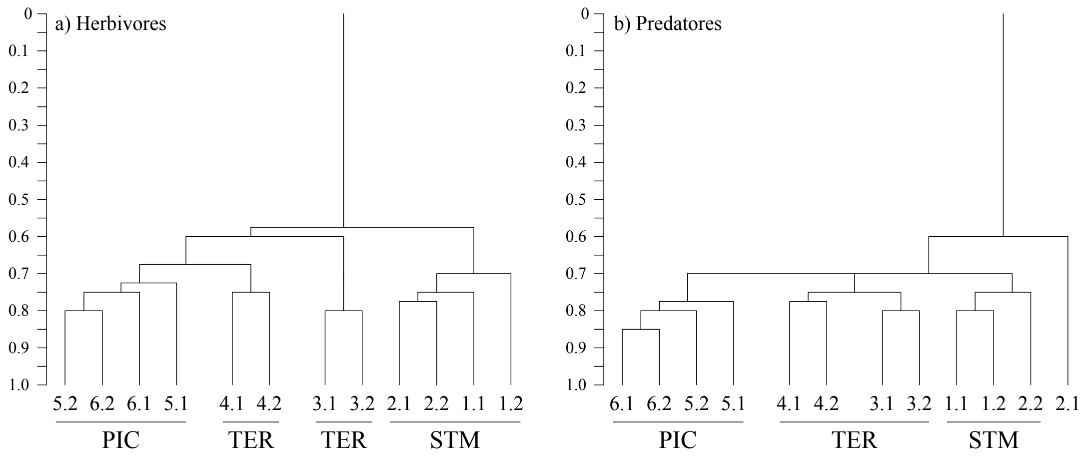

Fig. 5. Dendrograms of similarity (Sörensen's Index of Similarity) using: a) herbivores (data in Table 4); b) predators (data in Table 5). PIC = Pico; TER = Terceira; STM = Santa Maria.

In order to investigate the relationship between sites similarities for the vascular plants and arthropods, I plotted equivalent values of Sörensen's index for the plants and arthropods in regressions (Figs 6a, b and 7).

The similarity values obtained for each between-site comparison for vascular plants and herbivores are highly correlated ($r = 0.91$, $p = 0.0001$) (Figure 6a); the correlations are slightly lower (but still highly significant) for vascular plants and predatory arthropods (r = 0.84, p = 0.0001) (Fig. 6b), and for herbivorous and predatory arthropods (r = 0.84, p = 0.0001) (Fig. 7). The three regressions also show that the replicates are consistently similar in the three plotted groups, and that the similarities between the sites of Santa Maria and Pico generally have the lower values.

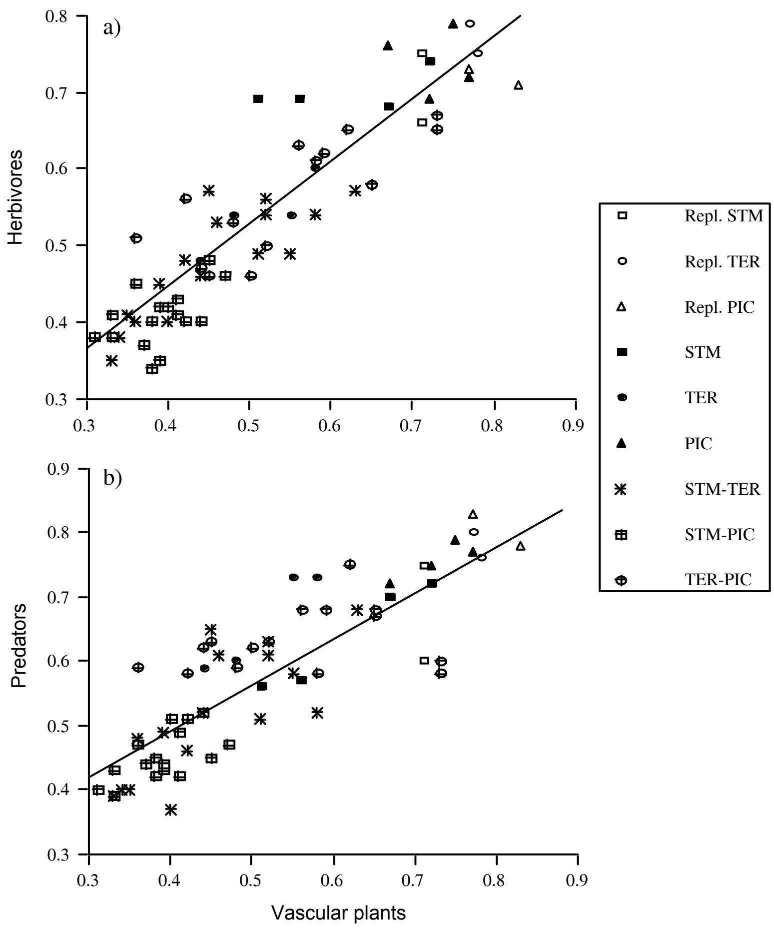

Fig. 6. Regressions of between-site similarity values for arthropods and that for vascular plants using values of Sörensen's Index of Similarity for each between-site comparison (values in Tables 3, 4 and 5). a) Herbivores ($y = 0.12 + 0.81x$; $r^2 = 0.83$, $p = 0.0001$); b) Predators ($y = 0.204 + 0.72x$; $r^2 = 0.71$, $p = 0.0001$); Repl. = replicates; STM = Santa Maria; TER = Terceira; PIC = Pico.

Finally, note that care is required in the interpretation of the correlation coefficients and probability levels in Figs 6 and 7, because the individual data points are clearly not independent (there are only 12 actual sample sites - the true replicates - but 66 data points in each figure). This is because each site is compared with every other site, to derive values for Sörensen's index, making the individual data points within any one taxon (vascular plants, or herbivores, or predators) non-independent. Nevertheless, the main pictures that emerge from Figs 6 and 7 are clear and unambiguous.

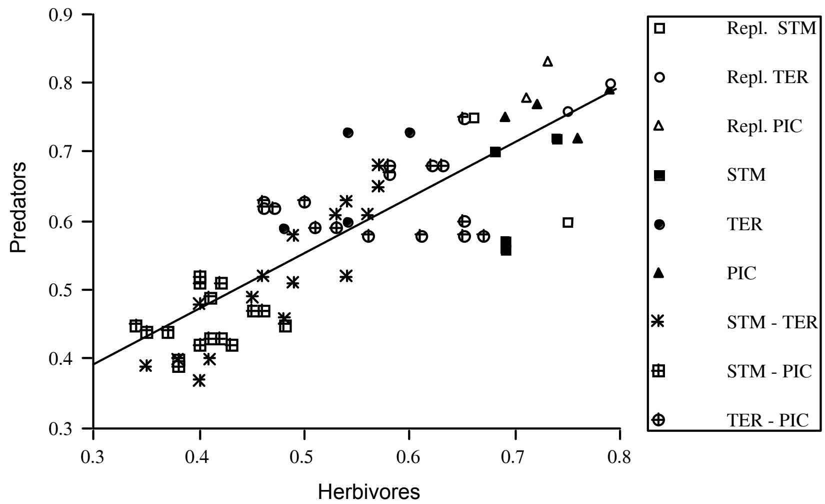

Fig. 7. Regression of between-site similarity values for predators and that for herbivores using values of Sörensen's Index of Similarity for each between-site comparison (values in Tables 4 and 5) ($y = 0.14 + 0.82x$; $r^2 = 0.71$, $p = 0.0001$); Repl. = replicates; STM = Santa Maria; TER = Terceira; PIC = Pico.

DISCUSSION

Analysis of the variation in composition of the vascular plants from 21 semi-natural pasture (SNP) sites showed unequivocally that the seven sites from each island form natural groups. In fact, the first TWINSPAN divisions grouped the sites by islands. Thus, differences in vegetation composition within an island were less important than differences between islands, implying that the two main sites of SNP on each island provided good representative "samples" of these SNP habitats in general. Two main end groups per island were obtained in the TWINSPAN analysis, the main two SNP being included, one in each group in Santa Maria and Pico. In Terceira, the fact that the three new SNP sites selected for this analysis are under a less intensive grazing management created a management discontinuity and grouped them together. The two main SNP sites from Terceira were grouped together with the respective outside field-site pasture permanent plots, which also implies that the 900 m^2 fenced sites are representative of the main large pasture site. A similar pattern was found in Santa Maria, but not in Pico. In Pico, despite sites 6.2 and "6.2 outside" being grouped together, site 6.1 is not in the same end group as "6.1 outside". This is probably a reflection of the topographical heterogeneity of site 6.1, where the occurrence of lava tubes and respective "skylights" creates different communities within the site, some more inaccessible to grazing and others more intensively grazed.

The overall percentage of indigenous (native + endemic) vascular plant species found in the 12 main studied sites (34%) is consistent with the overall pattern found in the archipelago, where only one third of the species of vascular plants are considered to be indigenous from the Azores (see HANSEN 1988; DIAS 1997). However, when the islands are individually analyzed, the patterns differ: endemic and native species are better represented in the field sites from Terceira and Pico and most of the species found in the sites from Santa Maria (78%) (56% in Terceira; 49% in Pico) are human post-colonization introductions. The small island of Santa Maria has been heavily impacted by people, no doubt resulting in this very high proportion of anthropochorous plant species. Moreover, the drier and more seasonal climate of Santa Maria also favours colonization by introduced annual and/or ruderal plants.

The effects of man are more evident in the plant species composition of the islands than in arthropod species composition. In fact, for the arthropods, the proportions of introduced species are lower overall, and quite similar among the three islands. Thus, habitat destruction through land clearance, which is more evident in Santa Maria, was not reflected in the arthropod fauna of the four study sites on this island. Further discussion on patterns of arthropod diversity are presented elsewhere (BORGES & BROWN 1999).

The study sites are not particularly rich in arthropod species when compared with continental pastures (see for comparison LUFF & EYRE 1988 - Curculionidae; LUFF et al. 1989 - Carabidae; CHERRILL & RUSHTON 1993 - Auchenorrhyncha; DOWNIE et al. 1995 - Araneae). However, the species richness of the study communities (237 species of arthropods sampled over five periods on three islands and 12 sites involving two types of pasture) must be compared with other data sets with caution because of differences in the types of habitats, sampling methods and numbers of sampling events.

There is a prevalence of common anthropochorous species, but also striking is the occurrence of numerous endemics. Three endemic species were classified as indicator species in the TWINSPAN analyses (see Fig. 3). The fact that the SNP from Santa Maria have a large proportion of introduced plant species, was not itself an obstacle to the occurrence of endemic arthropod species. Even a slow moving forest-dwelling species like the endemic Colydiidae *Tarphius depressus* was collected from site 2.1 (St. Espírito) (preliminary sampling period in March 1994) in pitfall traps. It is known that the input of fertilizers and pesticides and several other management practices are important in defining the quality of the pasturelands for the arthropods (RUSHTON & LUFF 1988; EYRE *et al.* 1989, 1990; RUSHTON *et al.* 1989, 1990, 1991; LUFF *et al.* 1990; CURRY 1994). The input of fertilizers to Azorean pastureland is, on average, about three times lower than average inputs to pastures on the European mainland (GARCIA & FURTADO 1991). This fact, together with generally low inputs in pesticides in the Azores, may mean that both SP and SNP are reasonably benign habitats for arthropods. Therefore, endemic arthropods were able to occur in the two pasture habitats, probably because they have similar levels of disturbance, i.e., low N inputs, similar numbers of grazing events, no pesticides.

TWINSPAN analyses showed that over local scale (between sites), medium scales (between habitats) or regional scales (between islands), the variation among pasture vascular plants and among arthropod assemblages was very different. In contrast to the plants, the arthropods showed a surprisingly homogeneous intra-island pattern. The altitude-climatic gradient, evident in the vascular plants, appears not to affect the arthropods, at least the predators. In fact, differences between habitats were not evident in the predatory arthropods, and it was necessary to consider the regional scale (islands) to find inter-community variation in indicator species composition. In the herbivore assemblage, the end group formed by the SP from Terceira (sites 3.1 and 3.2), however, is a reflection of the plant species composition and probably of the altitude-humidity gradient.

Differences in herbivorous arthropod species composition between SP and SNP in Terceira are not surprising. Due to more intensive and improved grazing management by the owners, the SP sites differ greatly in plant species composition and structure from SNP sites in Terceira. The fact that most of the indicator species of the SP sites from Terceira are human introduced grass-feeding species, probably reflects improved management practices.

The Importance Values for the vascular plants also showed some clear trends. The SNP of the three islands are dominated, in terms of relative frequency + relative density + relative cover (i.e. Importance Value) by the grass species *A. castellana* and *H. lanatus* and the native legume *L. uliginosus*. The only species common in most of the SP is the legume *T. repens*.

There is also a difference between SP and SNP in terms of densities of arthropod species. In fact, it is possible to group all the six SP sites by the occurrence of higher densities of the herbivore insect species *A. pisum* (Aphididae) and *A. rufus* (Thysanoptera; >> 10 m^{-2}) and the predator *A. analis* (Staphylinidae; >> 1.7 m^{-2}). The SNP are characterized by high densities of four herbivore species (the leafhopper *A. albifrons* (Cicadellidae; >> 1.5 m^{-2}), the delphacids *M. quadrimaculatus* and *Muellerianella* sp. a (Delphacidae) and *A. rufus* (Thysanoptera; >> 2 m^{-2})) and the predators *L. tenuis* (Araneae; >> 1.4 m^{-2}) and *A. analis* (Staphylinidae; >> 1.0 m^{-2}).

The results support the contention that the most similar sites in terms of plant species composition also have similar arthropod species assemblages. This result points to a high correlation between community structure of the vegetation and community structure of the arthropod assemblages. The present analyses highlight the role of plant species composition in invertebrate species composition.

PATTERSON & ATMAR (1986) coined the term "nested subset" to describe situations where species comprising a depauperate fauna should constitute a proper subset of those in richer faunas. There are a number of studies that have shown the importance of nested-subset analyses in community structure (see the review by WORTHEN 1996). An analysis of nestedness using the random models described in PATTERSON & ATMAR (1986) and CUTLER (1991) is beyond the scope of the present work, although there are indications in the data that the fauna of Terceira is a nested subset (sensu PATTERSON & ATMAR 1986) of the fauna of Santa Maria and that the fauna of Pico is a nested subset of the fauna of Terceira. Clearly, in these three Azorean islands similarity and nestedness reflect geographic proximity, but additional factors need also to be considered in deciding what determines the overall composition of the biotas (e.g. geological history; see BORGES & BROWN 1999).

In conclusion, the fact that Santa Maria is drier than the other islands, with a maximum altitude of only 587 m (86% of its area is under 300 m), is reflected mainly in plant species composition, where the high altitude sites (semi-natural pastures - SNP) were more similar to the low altitude sites from Terceira located at a similar absolute altitude but of a different habitat type (sown pastures - SP). One of the most important results of this work is the fact that such constraints of altitude and climate are much less evident in the arthropod fauna than in the flora. For arthropod assemblages, regional factors (the island itself) appear to be more important. Obviously, as already referred to above, plant species composition is important in defining arthropod species composition, but the regional (island) arthropod pool of species is also important in setting the species of arthropods occurring in pasture habitats.

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